

weak to be perceived on the tongue causes prolonged cardiac standstill.

The passage of a constant current through the interjugal part appears to cause an acceleration in the rhythm.

B. Effects of Vagus Stimulation on the Ostial Parts of the Sinus.

When either the right or left vagus nerve is stimulated the rhythmic power of both the right and left ostial parts is completely suspended for a time. The excitability to direct stimulation also is temporarily annulled; no contraction is caused by the application of even a powerful direct excitation.

As a secondary effect of vagus stimulation there often occurs a marked heightening in the rhythmic power of the ostial parts, and a consequent acceleration of the rate of the heart's action. Probably there is also in some instances an increase in the excitability of the ostial parts.

Weak or strong interrupted currents applied to the ostial part cause an immediate arrest of the heart's action, with the usual features of the inhibited state. Such a result is obviated by the administration of curare.

III. "On the Structure and Development of the Skull in the Mammalia. Part III. Insectivora." By W. K. PARKER, F.R.S.
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(Abstract.)

Although this paper is confessedly only a fraction of what is necessary to be done in this polymorphic order, it shows at least how difficult a group it is to handle. For the Insectivora are set in the midst of the other Mammalia—low and high. They might be called the Biological stepping-stones from the Metatheria to the Eutheria.

One thing can be done, even now, with our present fragmentary knowledge of the structure and development of the Insectivorous types—we can assure ourselves that these types are immediately above the Marsupials, that they have the Bats (Chiroptera) obliquely above them, that their nearest relations must be sought for amongst extinct Eocene forms, and that, lowly as they are, and arrested and often dwarfed to the uttermost (so that nature could not safely go further in that direction), they are rich in prophetic characters that have come to perfection in larger and nobler types.

I think it will not be denied that in the ascent of the types the Chiroptera are above the Insectivora, and, as it were, a sort of special

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"new leader" from that stock, and that the Insectivora are more or less transformed modifications of the Marsupial type. I suspect that the existing Insectivora just yield the zoologist one of his groups of types classed together because he knows not what else to do with them; they are not a proper, clear, special branch or "leader" of the Mammalian life-tree. They form one group under one designation, just as the *poor* of this metropolis form a group; their special mark is simply lowliness; they differ *inter se* almost as much as the whole remainder above them differ. The higher forms, however, because of their elevation, can afford to be subdivided again into order after order. If we could descend and see the transforming and newly transformed Placentalia of the Eocene epoch, then the morphologist and the zoologist would find common ground; the taxonomy of the latter, however, would be as useless as the titles and distinctions of modern society to some undeveloped race of savage men.

The evidently extreme specialization of the existing Monotremes or Prototheria, and their manifest close relationship to the Edentata—a strange lowly group of Eutherians, almost extinct in the old world, and not potent in genera and species in the new—makes it necessary for me in the present stage of my research to leave them until I have mastered both them and the great Marsupial sub-class. Of the latter, however, I can speak already, and as no interpretation of the meaning of the parts seen in a Eutherian skull can be made until they are read in the light of the structure of the *quasi-reptilian* skull of the Marsupial, I shall in this paper compare the two types together, using the lower and older, as a measure of the higher and newer, types of skull.

Anatomists are familiar with the character of the skull in adult Marsupials; to these may be added others that have turned up to me in the study of their development. When these are seen in the light of the types outside and below the Mammalia, then that which is typical in a high Mammal, as such, can be formulated, and the specialization of this great branch of the Vertebrate stock be understood. I will, therefore, here give a list of the more important and striking cranial characters of the Marsupials, promising to bring forward, as early as possible, figures and descriptions of the skull in various stages and in many kinds. But before making this comparison of the characters of the skull in the Marsupials with what is seen in the Insectivora, I will state that in the latter—a mere order—the diversity is fourfold that to be found in the Marsupials (which are worthy to be put not as a mere order, but as a sub-class), for in them, whether they be eastern or western kinds, the uniformity on the whole is very remarkable, as remarkable as the diversity seen in the Insectivora. The problem put to the morphologist, however, is to explain why the characters that distinguish a Marsupial from a high or Eutherian Mammal are for the most part those which the former

possess in common with the Sauropsida. The residuum of proper unique Metatherian characters neither to be found in the higher Mammals, on the one hand, or in the Sauropsida on the other, is but small. Another, and a crucial, difficulty is this—the Sauropsida, which of all others help us most in the interpretation of the Marsupial skull, are not those to be found in low Reptilian, but in the highest Avian, types. Of all birds the Passerinæ are the noblest, and are most marvellously specialized for their own peculiar mode of life, having many accomplishments and high intelligence. Yet it is from this order of birds that I have had most help in this matter, finding in their skulls special structures which closely correspond to what is most remarkable in that of the Marsupials. There are several characters in the *superficial* or *investing* elements of the skull of Marsupials that are unlike what we find in the higher forms of Placental Mammalia, but which linger in the lower.

a. The frontals are very small in proportion to the parietals, and the squamosals are, relatively, especially in the young, inordinately large—as large as the frontals.

b. The lacrymals are not only large, and have generally a facial plate, but they have, as a rule, *two* canals.

c. The palatine plates of the maxillaries and palatine bones form an extremely hollow or dome-like structure, and by the time the creature is full-grown much of their substance has been absorbed, so as to leave larger or smaller fenestræ: thus there is an attempt to return to the schizognathous condition of these parts seen in many Sauropsida.

d. The palatines are often formed of several pieces, very irregular patches of bone, and these irregular centres are largely absorbed, or united with the main parts in the adult skull.

e. The pterygoids are very small, and have their basicranial parts limited on account of the constant separate development of a large meso-pterygoid.

f. The main vomer is often relatively small; there is nearly always a pair of antero-lateral vomers protecting the cartilaginous capsules of Jacobson's organs, and large postero-lateral and often postero-medial vomers. These are very irregular and unsymmetrical, in the young *Cuscus*, especially, in which I find *ten* vomerine bones.

g. The floor of the tympanic cavity ossifies before the cartilage is ripe, but in two sub-equal centres—the annulus and “os-bullæ;” inside the latter a large folded cartilage protects the Eustachian tube, and outside the former the meatus externus is protected by a more or less segmented tube of cartilage, which ends outside in the continuous concha auris.

h. The jugal or malar bone is large, and reaches back so as to lie over the cartilage of the glenoid cavity, thus helping to form the joint.

i. The angular part of the lower jaw is greatly incurved forming a remarkable hollow inside.

In the *Endo-cranium* there are some very curious structures that differ from what we find in the high forms of Mammalia, but which mostly agree with what is seen in the Sauropsida.

a. The nostrils are sub-terminal, and give off large tongue-shaped cartilages to protect Jacobson's organs.

b. The whole nasal labyrinth is small, especially in the young, not more than half as large as in an average placental Mammal, and the cribriform plate is less depressed in front, very limited in size, and is square in form.

c. The orbitosphenoids do not form the presphenoid by meeting together below, but the presphenoid is as independent as the basisphenoid.

d. There is no special optic foramen in the orbitosphenoid, but the optic nerve passes through the common sphenoidal fissure with the orbital nerves and the first branch of the fifth; the second branch, like the third, has its own foramen rotundum, as in Man, and many other Eutheria.

e. The next character is one of the most important; it is this, namely, that the orbitosphenoids are flush with the alisphenoids. The latter, which are extremely large, ossify a tract of the general cartilaginous side-wall of the embryonic skull—the highly developed chondro-cranium—and not a *free flap* of cartilage, merely continuous with the basal bar, as in the Eutheria. For in these latter the more bulky brain pushes out the lower part of the side-wall of the skull, leaving for some time a band of cartilage, which runs free from the alisphenoid, passing from the orbitosphenoid up to the super-occipital. In front, the orbitosphenoid is confluent with the ethmoid, so that but for the breach in the wall made by the alisphenoid, there would be, even in placental Mammals, a chondro-cranium very similar to that of the Skate. This breach does not take place anywhere among the vertebrate types until we get above the Marsupials. The other character just mentioned, namely, the absence of a special optic foramen, is of similar import; there is no such a foramen in the "*Amniota*" until we are among the placental Mammalia.

f. The alisphenoid helps to form the drum cavity by developing behind its small external pterygoid process, a shell-like growth, similar to the "anterior tympanic recess" of Carinate birds. Thus, as the squamosal is a labyrinth of air cavities opening into the upper part of the drum cavity, these and the tympanic recess in the alisphenoid greatly enlarge the space for air. Indeed, not only those parts, but the mastoid region of the auditory capsule, and the sides and top of the occipital arch, all become pneumatic, as in *Crocodiles and Birds*.

g. The internal carotids pierce the basisphenoid submesially, that part of the basis cranii is not perforated in the middle, and the clinoid processes and cavity for the pituitary body are but little developed.

h. The limited, sub-erect, and flattish cribriform plates, and the small frontals, are the necessary correlates of a small brain cavity and brain. The *occipital plane* corresponds with those parts, being sub-erect; it forms but little more than a right angle with the general basi-cranial axis.

i. In the Marsupials as well as in the Monotremes we see the ossicle auditus, in making, so to speak. In all the sub-divisions of the class, Monotremes or Prototheria, Marsupials or Metatheria, and Placentals or Eutheria, the lower jaw is broken up, the longer part becoming the persistent mandible, the shorter hind part the *malleus*, whilst the starved and modified quadrate becomes the *incus*. For a long while in the growing Marsupial the malleus is manifestly a compound bone; it is an "articulare," with an internal and posterior angular process, as in the Fowl. On it the "angulare" can be seen, and sometimes, as in the half-grown Koala (*Phascolarctos*), a supra-angulare too. The working mandible, attached to a new pier on the jugal and squamosal, is composed of a sort of morphological mixture of a large *inferior labal cartilage*, a dentary bone, with coronoid and splenial regions, and the greater part of Meckel's cartilage—the *true primary ramus*.

j. The topmost segment of the next arch (pharyngo-hyal) is often a "columella," and not a *stapes*. In the early young and embryo of the Marsupials it is V-shaped; its greater front fork enlarging above to form the inverted base of the columella or stapes, and then dwindling into a rod; the lesser hind fork becoming, after a time, detached and then ossified, to form the interhyal. In fishes the uppermost element of a branchial arch (the hyoid is a branchial arch) often forks; in the Sturgeon these become two separate pieces, as in this particular case of the embryo Marsupial. There is not much to remark upon in the rest of the hyoid arch, the functional suspensory part.

For comparison with the Insectivora the *existing Marsupials* do not yield me all the archaic characters I want. For the existing low Eutheria are of course the descendants of Metatheria that were much more generalised and archaic than any now existing; these latter during the Tertiary Period must have undergone, on their own low platform, many adaptive changes that would make them look very strange beside the Marsupials of the Secondary epoch, if these latter could be restored for comparison with them.

The best type of Insectivore for general comparison is the Hedgehog (*Erinaceus europæus*), as it shows the least suppression of parts, and the best development of that which is diagnostic, so to speak, of the

order. In it the great investing bones of the skull are similar to those of the Marsupial, but the nasal and squamosals are smaller, and the frontals are larger. In the hard palate there is a considerable relapse, as in Marsupials; certain tracts of bone being absorbed, but it has no mesopterygoids, and only *five* vomers, yet the anterolateral pair are well developed. Moreover the tympanic region has only one annulus, the outer bone; there is no separate os-bullæ. Instead of the latter there is a crescentic shell of bone, which grows from the basisphenoid, greatly increasing the size of the tympanic cavity. In the endoskeleton in front of the tympanic cavity there is a remarkable ridge of bone growing outwards from the alisphenoid. That ridge is the remnant of the alisphenoidal tympanic wing of the Marsupial, and the shell of bone growing from the basisphenoid is the same morphological element as the separate os-bullæ, but it has lost its independence. The higher Mammalian type is fully reached in the thorough freedom of the alisphenoid from the general cranial wall. This character, indeed, is intensified into the special diagnostic of an Insectivore, for it lies almost wholly outside the orbitosphenoid. Here the sphenoidal fissure, which in this case lets out the second branch of the fifth, but not the optic nerve—that nerve having its own foramen in the orbito-sphenoid—is not a mere gap, but a *side passage*, or a sort of sphenoidal corridor, right and left. In these things the Hedgehog is higher than the Marsupial, but in some others it is lower, or more archaic. These latter characters, which suggest an uprise from a more general type than the existing Metatheria, are—

1st. The development of solid hyaline cartilage in the pterygoid region, a remnant of the pterygo-quadrate of the Ichthyopsida.

2ndly. The presence of a persistent pituitary hole, which is connected with a curiously specialized structure, only seen in typical Insectivores, namely, a hollowing out of the basis cranii beneath the pituitary region.

3rdly. A third archaic character, not seen in the existing Marsupials, is the huge relative size, long persistence, and separate distal ossification of Meckel's cartilage, so that in the embryo Hedgehog, and even in the nestling, the primary lower jaw is as large as in fishes generally, scarcely excepting the Selachians.

The ossicula auditus are typically Eutherian; we have lost the imperforate stapes or columella, the interhyal is very small or absent, and the malleus and incus are much like what we find in the higher Mammals, generally. The pneumaticity of the skull is much reduced: the olfactory region is almost double the relative size of that of a Marsupial. In the head of another family of the Insectivores, namely, the Mole (*Talpa europæa*) there is much that is in accord with what is found in its distant relation the Hedgehog, but in it there are evident signs of degradation and of relapse into what is Marsupial in

character. The nasal labyrinth is relatively immense, and the skull walls below, laterally, and behind, are as exquisitely pneumatic as in the Flying Marsupial (*Petaurus*), the Bird, or the Crocodile. The swollen basis cranii, all air galleries within, is so excavated that the hinder sphenoid, both base and wings, largely helps the flat single tympanic to form the drum cavity. The pituitary hole does not exist, but there is a considerable pterygoid cartilage. The ossicula in the adult are normal, but a curious special character is seen in the ossification, in the young, three parts grown, of the sheath of the stapedia artery, which for a time holds the stapes in its place. It is, however, absorbed afterwards, but remains in the related genus *Myogale*. In nearly half-grown young Moles the malleus is quite like that of the Marsupials; it is an evident "articulare," with copious wild growths of bone, sub-distinct, which answer to the "angulare" and "supra-angulare" of a Reptile or Bird. This malleus in its articular part has two endosteal and one ectosteal bony centre.

Meckel's cartilage, long continuous with the Malleus, is nearly as massive as in the Hedgehog, and has a more distinct separate ossification in its sub-distal part, a long, independent, but temporary *hypobranchial bone*.

The Mole shows a most remarkable development of the endocranium, which, twenty years ago, suggested to me that its skull retained unmistakable Monotrematous characters. In large young of the *Echidna* and *Ornithorhynchus* the solidity of the chondrocranium is immense, like that of a *Chimaeroid* Selachian, and the investing bones are thin and splintery. I have not made out the mode of ossification of the inner skull in those types, but in *spirit*, if not in the *letter*, the Mole agrees with them, that is, in the great development and independence of the inner skull. The opisthotic bone ossifies the normal petro-mastoid region, whilst the prootic bony centre begins in its right place on the front edge of the cartilaginous capsule, and then runs away from it into the wall of the skull. Thus there is a large bony tract in the temporal region between the squamosal and the large interparietal, which is not one of the ordinary ectocranial bones, but an endo-cranial bony tract overshadowing and yet imitating the true temporal bone or squamosal. This bone is represented by three separate centres in osseous fishes, namely, the prootic, pterotic, and sphenotic, whilst their true auditory region is partly ossified by the epiotic and opisthotic; the epiotic is only sub-distinct in the Mole. If I am asked why I dive so far down for my illustrations, instead of being satisfied with what Reptiles and Birds would show me, my answer is that these are often of no use for comparison, as they are as thoroughly specialized for their own mode of life as the Mammalia, generally, and are as completely, and often more completely, transformed from the original archaic type or types. Thus the Mole,

like most of the Edentata lately described by me, suggests as the root stock of the Eutheria, generally, not Marsupials (Metatheria), as we know them, but Prototherian forms in which, in ages long past, the existing Monotremes and Marsupials had a common origin. The Shrew (*Sorex vulgaris*) represents another family of the Insectivores, the Soricidæ. It combines the characters of the Mole and Hedgehog with peculiarities of its own that are manifestly due to dwarfing; many things are suppressed, as if there was not room in so small a skull for their development. The pituitary hole reappears, and the pterygoid cartilage, but the tympanic wings of the alisphenoid and of the basi-sphenoid are gone. The malleus does not show itself so unmistakably Marsupial, and Meckel's cartilage is slenderer. The sheathing alisphenoids are well seen, the squamosal is extremely small, low down, and devoid of a jugal process; the jugal bone is suppressed. The prootic wing is present, as in the Mole.

So much for the British representatives of these families of the Insectivora—the Erinaceidæ, Talpidæ, and Soricidæ. The Mascarene Insectivora are so evidently related to each other, as to suggest, at once, a common origin; these are the Centetidæ, the largest of which is the Tenrec (*Centetes ecaudatus*); the other genera treated of in this paper are *Ericulus*, *Hemicentetes*, and *Microgale*.

These are almost typical Insectivora, but they agree with the Shrews in having the jugal bone suppressed; they are also more Marsupial than our native kinds. In these types the normal characters of the skull of an Insectivore are combined with a remarkable Marsupial tympanic wing to the alisphenoid, but the os-bullæ is not free, it is merely an outgrowth of bone from the basisphenoid. The pituitary hole is present and in the large species the curious basi-cranial excavation; the optic foramina also and the sphenoidal side passages are remarkably developed. As in the genus *Phalangista* among the Marsupials, and *Sorex* and *Talpa* among the British Insectivora, the antero-lateral vomers are evidently suppressed, or have a very temporary independent existence; the postero-lateral vomers are rather small, as in the Hedgehog. In the embryo the main vomer is *relatively* as large as in the embryo Whale, and is curiously cellular or spongy. In nestlings this one primary azygous centre has broken up into three; one, the largest, above, and two lesser below, sheathing, it as it sheathes, the base of the nasal septum. Now this multiplication of the vomers, proper, is thoroughly Marsupial. It is unique, as far as I know, in the mode of its subdivision into secondary bony centres. In the African (Continental) family the Elephant or Jumping Shrews (Macroscelidæ), as illustrated by the largest forms *Petrodromus* and *Rhynchocyon*, we have a curious mixture of Marsupial or Metatherian and Eutherian characters, so that they are aberrant as Insectivores; the Marsupial characters are most remarkable:—

These are (1) the absence of an optic foramen in the embryo; (2) the alisphenoids scarcely overlapping the orbitosphenoids; (3) the tympanic wings of the alisphenoids are well marked, hollow shells in the embryo; (4) large antero-lateral vomers, and postero-lateral vomers, as large as in average Marsupials, and, as in many of them, meeting and uniting at the mid-line; (5) a large distinct "os-bul'æ," which makes a tympanic cavity as large as, and much like that of, *Petaurus* or *Phascoglossus*. On the high Eutherian side we have, in the embryo, frontals as large as the parietals, and strangest of all Mammalian specialization, a long *proboscis*, composed of thirty double rings of cartilage, a structure quite similar to the proboscis of an Elephant. The mesopterygoids are suppressed, but the pituitary hole is present.

I now come to a type for which no place can be found in our systems of Zoology, but for which the late Professor Peters, in despair, lodged with the Insectivora; I refer to the Flying Cat (*Galeopithecus*). This genus forms a Family by itself, and yet has only two species; it should form an Order, as the Hyrax does.

These two species of Flying Mammals are full of *remnants* of what is old, and *rudiments* of the new. I put them between the most archaic (Marsupials) and some of the most curiously modified Eutheria, the Frugivorous Bats, and survey them from these two widely separate standpoints; but they possess that which neither Phalanger nor Bat will account for or explain.

With a flat, outspread, foliaceous skull, as completely ankylosed as that of any bird, and as thoroughly pneumatic in its post-orbital region, we have one of the largest and most perfect *hard palates*; with the upper incisors partly suppressed, the lower incisors well developed and utterly unique, and the premolars and molars strong for grinding. The cheek bones and the squamosals are large and thoroughly Marsupial, so are the small external pterygoid processes and internal pterygoid bones, and the very large mesopterygoids. I find no antero-lateral vomers, but Jacobson's organs and their protecting cartilages are *twice as long* as in any types yet examined, and the postero-lateral vomers are almost as well developed as in Marsupials, whilst the main vomer is very large. The sphenoid bones are typically Eutherian, but the basisphenoid has beneath it, *as in Lizards*, a small "parasphenoid;" this I find only in *G. philippensis*, and as yet in no other Mammal. As in the Marsupials, the jugal or malar helps to form the glenoid cavity, and the squamosal is as large as in *Cuscus*, the lowest of the *Eastern Marsupials*. The single flat tympanic bone, with its ossified and compressed meatus, is very remarkable; but this part of the skull corresponds neither with the Marsupials nor the Insectivores, and this is true also of several other of its characters.

Those things in which it agrees with the Marsupials are not the same as in the Hedgehog; it differs from both Insectivores and Marsupials in its own peculiar way, and in some things is more archaic than either. This type appears to me to be a waif from a large group of forms that were beginning to be transformed out of the Metatheria into the Flying Eutheria (Chiroptera), certain of which, this living type among the rest, being arrested at the general level (or platform) of the Insectivora; they are equal to, rather than members of, the order Insectivora. The last type to be mentioned is the *Tupaia*, an Eastern form, rather high in position, yet combining characters for the first time seen in the Mammalia, namely, a perfect orbital ring, with old Metatherian structures, such as the large os-bullæ, the small external and internal pterygoids, and a somewhat absorbed hard palate. The last three kinds, *Rhynchocyon*, *Galeopithecus*, and *Tupaia*, all show a curious mixture of that which looks upwards to the highest types, and of that which has been retained from the lower and more archaic forms of the Mammalian class.

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